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Variation in tussock architecture of the invasive cordgrass *Spartina densiflora* along the Pacific Coast of North America

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Abstract Some introduced species spread rapidly beyond their native range and into novel habitats mediated by a high degree of phenotypic plasticity and/or rapid evolutionary responses. In this context, clonality has been described as a significant factor contributing to invasiveness. We studied the abiotic environment and the responses of different tussock architecture traits of the invasive cordgrass *Spartina densiflora* Brongn. (Poaceae). A common garden experiment and field studies of *S. densiflora* in salt marshes across a wide latitudinal gradient from California (USA) to British Columbia (Canada) provided a model system for an integrated study of the potential mechanisms underlying the response of

invasive *S. densiflora* populations to changes in environmental conditions. Our results showed that *S. densiflora* is able to adjust to widely variable climate (specifically, air temperature and the duration of the growing season) and sediment conditions (specifically, texture and hypoxia) through phenotypical plastic key functional tussock traits (e.g. shoot density, height, above- and below-ground biomass allocation patterns). Root biomass increased in coarser sediments in contrast to rhizomes, which were more abundant in finer sediments. Above-ground biomass and leaf area index increased mainly with air temperature during summer, and more robust (taller and wider) shoots were associated with more oxygenated sediments. In view of our results, *S. densiflora* appears to be a halophyte with a high degree of phenotypic plasticity that would enable it to respond successfully to changes in the abiotic conditions of salt marshes driven by global climate change, such as increasing salinity and temperatures.

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Introduction

Some introduced species are able to spread rapidly beyond their native range and into novel habitats encompassing a wide range of environmental conditions. Two main mechanisms may explain this

behavior: a high degree of phenotypic plasticity of the invading species, and/or rapid evolutionary responses by invasive populations (Gioria and Osborne 2014; Matesanz et al. 2010). Increased understanding of these two mechanisms would allow us to better identify environmental changes that promote invasiveness, predict future invasions, and manage existing invasions (Daehler and Strong 1996; Drenovsky et al. 2012).

The clonal growth strategy contributes to clonal plant dominance in many ecosystems and has been implicated as a significant factor contributing to invasiveness (Martina and von Ende 2013). Genets have been demonstrated to be locally adapted to their environment in terms of morphology (e.g. Prati and Schmid 2000) or to have environmentally based variation in functional traits (e.g. Roiloa et al. 2007). Therefore, determining intraspecific variations in tussock traits that shape clonal architecture, such as biomass distribution, shoot height and density and leaf area index (LAI) is essential to understanding the invasive capacity of clonal exotic plants.

The invasion of the halophytic South American cordgrass *Spartina densiflora* Brongn. (Poaceae) across a wide latitudinal gradient from California (USA) to British Columbia (Canada) provides a natural model system for an integrated study of the potential mechanisms underlying the response of invasive populations to substantial variation in climate and other environmental variables. *S. densiflora* is native to the South Atlantic coasts of Brazil and Argentina, where it occupies a wide variety of habitats from 23°20'S to 51°33'S latitude. *S. densiflora* has invaded salt marshes in Chile (ca. 33°30'S–42°46'S), Morocco (ca. 34°50'N), the southwest Iberian Peninsula (ca. 36°02'N–37°21'N), and the Pacific Coast of North America from San Francisco Bay, California (ca. 37°56'N) north to Vancouver Island, British Columbia (ca. 49°20'N) (Bortolus 2006; Saarela 2012). Invasive populations of *S. densiflora* show a high degree of phenotypic plasticity in foliar traits along the Pacific Coast of North America (Castillo et al. 2014) and in characteristics of root systems in South America (Daleo and Iribarne 2009), probably related to the ancient hybrid origin of this species (Fortune et al. 2008). Furthermore, ecotypic differentiation related to environmental changes driven by latitude and elevation along the tidal gradient have been described for populations in its native range

(Álvarez et al. 2009; Di Bella et al. 2014), even though these native populations have low detectable genetic variation (Ayres et al. 2008). This low genetic variation may be even more accentuated, through the founder effect, for recently introduced *S. densiflora* invasive populations that are rapidly spreading along the Pacific Coast of North America through hydrochorous dispersal (Howard and Sytsma 2013). These populations are facing quite different abiotic conditions both in the atmospheric environment (e.g. changes in air temperature and growing season length) and in the sediment environment (e.g. variations in salinity and oxygenation levels) (Castillo et al. 2014).

We hypothesized that variation in tussock traits within populations of *S. densiflora* from a geographic gradient along the Pacific Coast of North America would primarily be due to phenotypic plasticity, rather than adaptive differentiation. To probe this hypothesis, we compared tussock traits from five populations at invaded field sites along the Pacific Coast with those populations grown in a common garden experiment. Integrated biogeographical approaches that include the study of natural populations along latitudinal gradients, paired with methods such as common garden experiments, are a way to increase our understanding of responses of plant species to environmental change (De Frenne et al. 2013), to understand exotic plant invasions (Hierro et al. 2005), and to test whether inter-population differences recorded in the field are due to genetic differentiation or phenotypic plasticity (Castillo et al. 2005a).

Methods

Study sites

Our field study was carried out in summer 2010 at five estuarine marshes invaded by *Spartina densiflora* along the Pacific Coast of North America. Our five study populations, fully described in Castillo et al. (2014), span the entire known latitudinal range of *S. densiflora* on this continent, and occur in a variety of estuarine environments including riverine, embayments, and sounds (FGDC 2012). The southernmost *S. densiflora* population evaluated was in San Francisco Bay at Corte Madera, California (37°56'33"N, 122°30'55"W) in a middle elevation salt marsh. At Humboldt Bay we studied the invasion of *S. densiflora*

in a middle intertidal elevation marsh located in the northern portion of the bay (40°49'53"N, 124°10'17"W). Spicher and Josselyn (1985) speculated that this population was introduced to Humboldt Bay by ships from Chile that arrived for lumber trade during the late nineteenth century, and subsequently colonized 90 % of the estuary's salt marshes (Pickart 2001). To the north of Humboldt Bay, our third study site was in the narrow, fringing intertidal zone of the Mad River estuary (40°56'10"N, 124°7'48"W). On the Washington Coast, we included the invasive population first documented by Pfauth et al. (2007) at Grays Harbor Estuary (46°57'N, 124°8'08"W). The final population at our northernmost site was in a fringing salt marsh along the narrow Baynes Sound channel on the East Coast of Vancouver Island, British Columbia, Canada. This population, discovered in 2005 (Morgan and Sytsma 2010), occupies an intertidal cobble plain dominated by *Salicornia pacifica* (Standley) A. J. Scott (49°33'N, 124°52'09"W).

The five population sites all experience mixed tides. The climate gradient ranges from Mediterranean in the south with cool, wet winters followed by hot, dry summers (but with summer fog), to maritime west coast climate with cooler, foggy summers for the other USA locations. At the northern extreme, the Vancouver Island site has a wider temperature range with lower low temperatures during winter but less summer fog than the other population sites. Mean daily year-round temperature varies between 9.7 and 17.7 °C for San Francisco Bay, 8.8–14.8 °C for Humboldt Bay, 5.6–16.1 °C for Grays Harbor and 2.7–18.0 °C for Vancouver Island (1971–2000 climate series data). Vancouver Island has the lowest mean minimum daily temperature among sites in January (−0.8 °C); mean temperatures have been similar for every location during June and July (ca. 11 °C) (Environment Canada 2002; NCDC 2004).

Spartina densiflora habitat evaluations

We used hand-held GPS technology to record specific geographic coordinates for every population site. Meteorological conditions were characterized using mean daily temperature (°C) for the week before our field evaluation visits as reported in local climatological stations (NCDC 2013). We acquired publically available data to characterize mean daily global horizontal insolation ($W\ h\ m^{-2}$) for the month (NREL

1992; NRC 2009), day-length (h) (Lammi 2008), and the number of annual growing degree days (reflecting both temperature and duration of the growing season) for all sites (Environment Canada 2002; NCDC 2004). We used 10 °C as a threshold for growth of *S. densiflora*, which was applied previously for the congener *Spartina alterniflora* Loisel. (Kirwan et al. 2009). We obtained mean tidal level and range (m) for each location from NOAA Tide Predictions and Fisheries and Ocean Canada.

Spartina densiflora populations were visited during low-tides. Sediment redox potential (Eh) was determined in the field at ten random sampling points (portable meter, Orion pH/mV 290A). Sediment cores (5 cm diameter, 0–10 cm depth) were collected, stored in sealed containers and transported to the laboratory. Sediment was mixed in a 1:1 ratio with distilled water to determine electrical conductivity (Hanna Instruments 9033) and pH (Orion pH/mV 290A) ($n = 10$ per site). Loss on ignition (LOI) was used to estimate sediment organic matter concentration ($n = 10$). Gravel percentage was recorded gravimetrically in relation to the other sediment fractions. Percentages of sand, silt and clay were recorded using a hydrometer method ($n = 3$) (Gee and Bauder 1986). Nitrogen concentration was measured on dried and ground sediments ($n = 10$) using a Perkin Elmer 2400 CHN/O elemental analyzer (Waltham, MA, USA).

Tussock traits

Ten adult tussocks of *Spartina densiflora* with between 10 and 80 live shoots and a mean tussock area between 15 and 41 cm² (ca. 2–3 years old) were randomly selected and individually marked in each of the five populations. Random samples were separated by a minimum of 1 m in an effort to sample potentially different genotypes. The following tussock traits were recorded for the marked tussocks in the field ($n = 10$ tussocks): (1) live, spiked, and dead shoot density; and (2) height and diameter of live shoots (5 randomly selected shoots per tussock). Shoot height was measured from the base of the shoot to the tip of the tallest leaf, and shoot diameter was recorded at the base of the shoot using calipers.

Ten entire tussocks, similar in size to those marked, were also collected from each population. Rhizomes and roots, which grew from rhizomes, were washed carefully to remove sediment. Biomass of roots,

rhizomes, dead shoots with leaves, live shoots without leaves, and live and dead leaves of live shoots were recorded in the laboratory after drying samples in a forced-air oven at 80 °C for 48 h. The dry weights (DW) of the different organs per plant ($n = 10$ tussocks per population) were obtained, and total standing above-ground and below-ground biomass (AGB and BGB, respectively) and AGB:BGB ratio were calculated. Rhizomes were oven-dried, ground and then analyzed for total nonstructural carbohydrates (TNC; in mg g^{-1} DW) using a modified procedure by Swank et al. (1982). TNC extracts were incubated at 55 °C for 15 min with one unit of amyloglucosidase (Sigma A-3042) per milliliter of completely hydrolyzed starch (Owens and Madsen 1998). The samples were assayed for reducing sugars using a photometric adaptation of the Somogyi method (Nelson 1944). In addition, LAI was obtained recording total leaf area and the area covered by each plant ($n = 10$ tussocks). To calculate total leaf area per plant, we used the weight of five leaf drilled circular pieces with a known area (0.5 cm diameter) and the recorded live leaf dry mass per plant (Carrión-Tacuri et al. 2011).

Common garden experiment

Every tussock of *Spartina densiflora* measured in the field study was collected and rhizomes were separated and grown in perlite substrate for 27 months (plastic pots: 20 cm diameter $\times$ 18 cm height) in a greenhouse at the University of Seville, Spain (37°21'42"N, 5°59'15"W). Pot bases were kept permanently flooded to a height of 2 cm, and watered with 20 % strength modified Hoagland's nutrient solution (Hoagland and Arnon 1950; Epstein 1972). Solutions were changed once a week. After 27 months of growth, every tussock trait recorded in the field, except below-ground biomass, was recorded again for the same plants acclimated to common greenhouse conditions to assess if the differences observed in the field reflected phenotypic plasticity or population differentiation. Common greenhouse conditions included substrate Eh of 234 ± 5 mV, pH 8.3 ± 0.2 , electrical conductivity 0.5 ± 0.0 mS cm^{-1} , mean monthly air temperature 23 ± 2 °C and mean monthly air relative humidity 62 ± 2 %. Light conditions of mean radiation of $700 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ at canopy level and a daily photoperiod of 16 h (that was extended with incandescent lights, Osram Vialox NAV-T (SON-T)

400 W, giving a continuum spectrum) were set up to imitate those recorded at higher latitude sites during summer in relation to photoperiod and light intensity. *Spartina densiflora* is a facultative halophyte that can germinate, establish, and develop in freshwater conditions (Nieva et al. 2001a; Castillo et al. 2005b). Fresh water was used to avoid salinity effects on tussock growth, since salinity has a significant effect on *S. densiflora* growth and biomass allocation (Grewell et al. 2015).

Data analyses

Statistical analyses were carried out using SPSS 12.0 (SPSS Inc., Chicago, USA). Deviations were calculated as standard error of the mean (SEM). Data were tested for homogeneity of variance and normality with the Levene test and the Kolmogorov–Smirnov Test, respectively ($P < 0.05$). When homogeneity of variance between groups was not found, data were transformed using $\ln(x)$ function. If homogeneity of variance was not achieved by data transformation, then the means were compared using Kruskal–Wallis H-test and Mann–Whitney U-test. Tussock traits were compared among *S. densiflora* populations by one-way analysis of variance (ANOVA) using the geographic location of populations as the grouping factor (F-test). Tukey's Honest Significant Difference (HSD) test between two means was calculated only if the F-test was significant at the 0.05 level of probability. Principal Components Analysis (PCA) was performed to reduce the number of abiotic and tussock trait variables in the field, analyzing the correlation matrix with 25 maximum iterations for convergence without rotation to extract independent PC factors with eigenvalues >1 . Multiple linear regression analyses were used to characterize the relationships between PCA factors of the abiotic environment (A) with PCA factors of tussock traits (T). Simple linear regression analyses were used to characterize the relationships between abiotic variables and tussock traits.

Results

Abiotic environment in the field

Four factors were obtained for the abiotic environment from the PCA, explaining 86.0 % of the variance. The

first factor (PC1-A) was positively correlated with latitude, day length (varying between 14 h 47' at San Francisco Bay and 15 h 56' at Vancouver Island), mean tidal level (changing between 0.96 and 1.67 m at San Francisco Bay and Vancouver Island, respectively) and coarse substrates (sediments with higher sand and gravel percentages and lower clay percentage), and negatively with the number of growing degree days (ranging from 924 for Vancouver Island and 3029 for San Francisco Bay). PC2-A was positively correlated with mean tidal range [minimum at San Francisco Bay (1.26 m) and maximum at Grays Harbor (2.20 m)] and negatively with more anoxic (Eh between -203 ± 67 mV at Grays Harbor and $+191 \pm 21$ mV at San Francisco Bay) and acidic sediments (pH varied narrowly between 6.3 ± 0.1 at Grays Harbor and 7.2 ± 0.1 at Vancouver Island) exposed to less mean daily isolation (ranging between 4964 W h m^{-2} at Grays Harbor and 6322 W h m^{-2} at San Francisco Bay). PC3-A was positively correlated with saltier sediments (electrical conductivities ranging from $0.2 \pm 0.0 \text{ mS cm}^{-1}$ at Mad River and $13.8 \pm 0.7 \text{ mS cm}^{-1}$ at San Francisco Bay) and mean daily temperature [minimum at Grays Harbor (12.3°C) and maximum at Vancouver Island (20.3°C)], and PC4-A negatively with the silt percentage. Detailed data on the abiotic environment are shown in Castillo et al. (2014).

Tussock traits

Tussock architecture traits (Fig. 1) and biomass production and allocation data (Fig. 2) varied widely among measured plants from field populations. Five factors were obtained for the tussock traits in the field from the PCA, explaining 77.7 % of the variance (Table 1; Fig. 3). The first factor (PC1-T) was positively correlated with above-ground biomass (AGB) (marked by live leaf and live shoot biomass, which varied between $1972 \pm 298 \text{ g m}^{-2}$ for Mad River and $6866 \pm 622 \text{ g m}^{-2}$ for Vancouver Island), LAI (varying between 0.36 ± 0.04 for Grays Harbor and 2.49 ± 0.31 for Vancouver Island) and root biomass (varying between $512 \pm 81 \text{ g m}^{-2}$ for Mad River and $1228 \pm 127 \text{ g m}^{-2}$ for Vancouver Island) (Table 1; Fig. 3). Above-ground biomass increased with live shoot density ($r = 0.442$, $P < 0.001$, $n = 50$) and leaf area index (LAI) ($r = 0.824$, $P < 0.0001$, $n = 50$) and decreased with the number of live leaves

($r = -0.461$, $P < 0.001$, $n = 50$). Above-ground biomass also increased with root biomass ($r = 0.656$, $P < 0.0001$, $n = 50$).

The second factor (PC2-T) was positively correlated with rhizome biomass, dead shoot biomass, BGB (varying between $1617 \pm 255 \text{ g m}^{-2}$ for Grays Harbor and $3678 \pm 946 \text{ g m}^{-2}$ for Humboldt Bay) and AGB:BGB ratio (Fig. 3). The third (PC3-T) was positively correlated with live shoot diameter (varying slightly between $3.1 \pm 0.1 \text{ mm}$ for Grays Harbor and Humboldt Bay and 3.4 ± 0.1 for Vancouver Island) and height (varying markedly between $29.4 \pm 2.0 \text{ cm}$ for Grays Harbor and $46.4 \pm 1.9 \text{ cm}$ for Vancouver Island), and the fourth (PC4-T) positively with rhizome TNC (changing between $83 \pm 8 \text{ mg g}^{-1}$ DW for Mad River population and $141 \pm 9 \text{ mg g}^{-1}$ DW for Humboldt Bay population; ANOVA, $F_{4,45} = 3.857$, $P < 0.01$) and spiked shoot density (Figs. 1, 2, 3; Table 1).

Each tussock trait showed significant inter-population differences in the field. Nearly all of these inter-population differences disappeared in the common garden experiment. Just two interpopulation differences were recorded in the common garden experiment, without showing any common behavior with data recorded in the field. Live shoot density of plants from San Francisco Bay was lower than from Grays Harbor and spiked shoot density was higher for San Francisco Bay than for the other populations (ANOVA or Kruskal–Wallis H -test, $P < 0.05$; Figs. 1, 2).

Relationships between environmental factors and tussock traits

PC1 for tussock traits (PC1-T) correlated positively with PC1-A and PC3-A (Table 2). Thus, tussocks accumulating more roots, more AGB and with higher LAI were growing on coarser sediments at higher latitudes with higher air temperatures during summer (Figs. 4, 5).

PC2-T decreased with PC1-A and increased with PC4-A (Table 2), reflecting that tussocks with higher BGB (marked by higher rhizome biomass) were growing in more finely-textured sediments at higher latitudes, influenced mainly by more growing degree days (Fig. 4).

PC3-T decreased with PC2-A, reflecting that live shoot diameter and height increased in more oxygenated and less acidic sediments exposed at lower

Fig. 1 Live, spiked and dead shoot density (shoot m^{-2}), live shoot height (cm), live shoot diameter (mm), number of live and dead leaf per live shoot, and leaf area index (LAI) for five *Spartina densiflora* invasive populations from five locations along the Pacific Coast of North America (Vancouver Island, Grays Harbor, Mad River, Humboldt Bay, San Francisco Bay) growing in the field (black bars) and in a common garden experiment (white bars). Data are mean $\pm$ SEM ($N = 10$). Different letters indicate significant differences between populations in the field or in the common garden experiment (ANOVA and Tukey-HSD test or Kruskal–Wallis H-test and Mann–Whitney test, $P < 0.05$)

mean tidal ranges and more mean daily isolation, and PC4-T correlated positively with PC2-A and slightly with PC3-A ($P < 0.05$), showing that rhizomes with higher total nonstructural carbohydrates (TNC) and higher spiked shoot densities were recorded at saltier, more anoxic and acidic sediments exposed to higher air temperature and insolation during summer (Fig. 6; Table 2).

Discussion

The South American cordgrass *Spartina densiflora* has invaded habitats with a wide range of environmental conditions along the Pacific Coast of North America. Our results show that the architectural traits of clonal tussocks from these invasive populations are phenotypically plastic in their response to widely variable climate (specifically, air temperature and the duration of the growing season) and substrate conditions (specifically, texture and hypoxia), which suggests that they have the ability to continue to adjust with future climate changes.

The production and allocation of biomass recorded for *S. densiflora* were in the range reported previously for this and other *Spartina* species (Castillo et al. 2010). Root biomass increased in coarser sediments, whereas rhizomes were more abundant in finer sediments. These results are consistent with previous studies reporting higher root development in order to exploit more soil volume for nutrients in coarse-textured and poor sediments than in fine-textured and fertile sediments (e.g. Wang et al. 2014). Similar tradeoffs between *Spartina* organs have been described previously between rhizomes, above-ground biomass (AGB) and seed production (e.g. Verburg and Grava 1998; Wang et al. 2008). In

addition, root biomass increased with summer air temperature and rhizome biomass increased with the duration of the growing season (the number of growing degree days). Generally speaking, roots in grass species have high turnover rates (e.g. Xiong and Katterer 2010) and are therefore sensitive to short-term environmental changes such as increases in temperature during summer. In contrast, rhizomes are long-lived structures that would be influenced mainly by long-term stable environmental conditions such as the duration of the growing season. Root biomass of opportunistic invasive species, such as *S. densiflora*, can increase with temperature due to increasing soil nutrient availability through accelerated microbial activity (Thakur et al. 2014). Daleo and Iribarne (2009) reported that *S. densiflora* shows a high plasticity in its root system development between anoxic and well-aerated sediments, allocating most of its root biomass to the first centimeters of soil in anoxic sediments and showing a root biomass more homogeneously distributed in oxygenated soils. In our study, rhizome biomass was around two times higher, and AGB:BGB ratio was almost two times lower, at lower than at higher latitudes, probably due to longer growing seasons that allowed higher carbohydrates reserve accumulation to counter harsh conditions in the salt marshes. This result contrasts with previous studies that found higher allocation to storage organs in dicot species with northward range expansions (Jia et al. 2010; Sawada et al. 1994), but it is in accordance with D'Hertefeldt et al. (2014) who showed that *Aegopodium podagraria*, a clonal herb with a high phenotypic plasticity, accumulates more rhizomes at lower latitudes. Total nonstructural carbohydrates (TNC) concentrations in rhizomes decreased with lower salinities (lower electrical conductivities), which could reflect the depletion of rhizome reserves due to growth stimulation under brackish conditions, where *S. densiflora* has been described as a highly competitive species (Costa et al. 2003). Depletion of carbohydrate reserves during rapid growth has been reported in several other submersed and emergent aquatic plants such as *Phragmites australis* (Granéli et al. 1992; Čížková et al. 2001), *Egeria densa* (Pennington and Sytsma 2009), and *Myriophyllum spicatum* (Perkins and Sytsma 1987; Madsen 1997). Rhizome dynamics are very important in salt marsh development in a changing world since rhizome accumulation is key to maintaining soil volume with

Fig. 2 Biomass of root, rhizome, below-ground organs, live and dead shoot, live and dead leaf and above-ground organs (g m^{-2}) for five *Spartina densiflora* invasive populations from five locations along the Pacific Coast of North America (Vancouver Island, Grays Harbor, Mad River, Humboldt Bay, San Francisco Bay) growing in the field (*black bars*) and in a common garden experiment (*white bars*). Data are mean $\pm$ SEM ($N = 10$). *Different letters* indicate significant differences between populations in the field or in the common garden experiment (ANOVA and Tukey-HSD test, $P < 0.05$). *Not recorded

increasing sea level rise (Wigand et al. 2014) and because investment of resources in rhizomes contributes to the ability of invasive clonal plants to establish in a wide range of habitats (Price et al. 2001).

Above-ground biomass and leaf area index (LAI) of *S. densiflora* increased with temperature during summer. The highest values of AGB (primarily biomass of live shoots and leaves) and LAI were recorded for the Vancouver Island population, the most northern location, but, interestingly, the location with the warmest summer temperatures. Low temperatures should constrain C-4 photosynthetic metabolism of *S. densiflora* since phosphoenolpyruvate carboxylase activity is reduced at lower temperatures (Lara et al. 2001). Previous studies on *Spartina* species have described a relationship between biomass production

and air temperature (Giurgevich and Dunn 1979; Drake 1989; Duarte et al. 2013). On the other hand, AGB increased together with root biomass, which could reflect a higher nutrient uptake favoring aerial biomass production. Biomass production of grasses depends mainly on three structural characters: blade size, shoot density and number of green leaves per tiller (Lemaire and Chapman 1996). In the case of *S. densiflora* along the broad range of latitude represented by our study sites, AGB increased in those populations with higher shoot densities and higher LAI (marked by fewer but larger leaves).

Our results are similar to those recorded along the Atlantic Southwest Coast of South America, where *S. densiflora* is native and its AGB is reduced by climatic restrictions (Montemayor et al. 2014). Nevertheless, *S. densiflora* AGB in its native range is inversely correlated with latitude since xeric conditions and salinity increase at higher latitudes (Isacch et al. 2006; Montemayor et al. 2014), and the population at the highest latitude in our study had the highest AGB and salinity did not have a significant relationship with AGB. Humid climatic conditions dominated at our high latitude site on Vancouver Island, and no hypersaline conditions were recorded. *S. densiflora* is a halophyte with a high tolerance to salinity (Maricle et al. 2007), but its growth is limited in

Table 1 Factor loadings (PC-T) of the individual variables obtained by a principal component analysis (PCA) on *Spartina densiflora* tussocks traits from 5 populations along the West Coast of North America from San Francisco Bay to Vancouver Island

	PC1-T	PC2-T	PC3-T	PC4-T
Above-ground biomass	+0.972	+0.063	−0.091	−0.036
Live shoot biomass	+0.963	−0.140	−0.029	+0.009
Live leaf biomass	+0.942	−0.035	−0.085	−0.114
Dead leaf mass	+0.889	−0.144	−0.090	+0.017
Leaf area index	+0.876	+0.026	+0.126	−0.169
Root biomass	+0.724	+0.268	+0.127	−0.232
Live shoot density	+0.527	−0.297	−0.314	+0.086
AGB:BGB ratio	+0.466	−0.613	−0.341	+0.193
Below-ground biomass	+0.365	+0.888	−0.051	−0.058
Live shoot height	+0.324	+0.170	+0.756	+0.132
Spiked shoot density	+0.312	+0.259	+0.452	+0.666
Rhizome biomass	+0.204	+0.921	−0.093	−0.049
Rhizome TNC	+0.174	−0.015	+0.003	+0.783
Live shoot diameter	−0.021	−0.253	+0.695	−0.338
Dead shoot mass	−0.075	+0.861	−0.181	−0.074
Dead shoot density	−0.218	+0.581	−0.235	+0.247
<i>Eigen values</i>	5.797	3.458	1.629	1.410
<i>Explained variance</i>	36.2	21.61	10.2	8.8

Correlations between the PCA and leaf traits with factor loadings $> \pm 0.600$ are marked in bold

Fig. 3 Principal Components Analysis (PCA) plot of tussock traits in five *Spartina densiflora* invasive populations along the Pacific Coast of North America (open inverted triangle Vancouver Island, open triangle Grays Harbor, filled diamond

Mad River, filled square Humboldt Bay, filled circle San Francisco Bay). Vectors: 1 Above-ground biomass, 2 Root biomass, 3 Above: below-ground biomass ratio, 4 Below-ground biomass, 5 Rhizome biomass, 6 Dead shoot biomass

Table 2 Correlation matrix [Pearson correlation coefficient (r) and probability level (P)] between factors loadings coming from Principal Components Analyses for abiotic environmental variables (PC-A) and for tussocks traits (PC-T) for five *Spartina densiflora* invasive populations along the Pacific Coast of North America ($N = 50$)

	PC1-A	PC2-A	PC3-A	PC4-A
PC1-T				
$r =$	+0.566	-0.204	+0.555	+0.047
$P <$	0.0001	0.155	0.0001	0.747
PC2-T				
$r =$	-0.472	-0.108	+0.201	+0.457
$P <$	0.0001	0.454	0.163	0.001
PC3-T				
$r =$	+0.060	-0.393	+0.115	+0.066
$P <$	0.677	0.005	0.427	0.648
PC4-T				
$r =$	-0.223	+0.393	+0.354	+0.174
$P <$	0.120	0.005	0.012	0.227

Correlations with $P < 0.05$ are marked in bold

hypersaline conditions (Castillo et al. 2005b). As in our study, salinity was not directly related to biomass accumulation of *Spartina maritima* along a latitude gradient in Portugal (Duarte et al. 2013). The leaves of *S. densiflora* at Vancouver Island were at a suboptimal state with low photosynthetic pigments concentrations

(Castillo et al. 2014) that could compensate with functional tussock traits such as higher LAI and higher tiller densities leading to higher AGB accumulation. In view of these results, it is expected that *S. densiflora* invasion would be faster at Vancouver Island where summers are mild in comparison to the other invaded estuaries to the South.

More robust (taller and wider) shoots were found growing on more oxygenated sediments. Previous studies have described *S. densiflora* as a halophyte whose germination, distribution, physiology and biomass are limited by anoxia along the tidal gradient (Castillo et al. 2000, 2008; Mateos-Naranjo et al. 2008; Abbas et al. 2012, 2014; Di Bella et al. 2014). This behavior contrasts with that of halophytes that are well-adapted to low marsh conditions, such as *Spartina maritima* (Curtis Fernald, which increased its shoot height through phenotypic plasticity when growing on anoxic sediments (Castillo et al. 2005a).

Every population converged in almost all tussock architecture traits when growing in a common environment, suggesting that environmental conditions and phenotypic plasticity largely determine tussock traits in *S. densiflora* on the Pacific Coast of North America. These *S. densiflora* populations also have high phenotypic plasticity in leaf traits (Castillo et al. 2014), and to increasing salinity that can be expected with increased global warming and sea level rise

Fig. 4 Relationships between rhizome biomass and sediment sand content and growing degree days, and between root biomass and sediment gravel content and mean daily air temperature during last week before sampling for tussocks from

five invasive populations of *Spartina densiflora* along the Pacific Coast of North America. Populations: *SF* San Francisco Bay Estuary, *HB* Humboldt Bay Estuary, *MR* Mad River Estuary, *GH* Grays Harbor Estuary, *VI* Vancouver Island

(Grewell et al. 2015, this issue). Abbas et al. (2012) also reported high physiological plasticity for *S. densiflora* seedlings in response to flooding. The considerable phenotypic plasticity in *S. densiflora* is consistent with that found in *S. anglica* (Thompson et al. 1991), *S. foliosa* (Trnka and Zedler 2000) and *S. alterniflora* (Elsey-Quirk et al. 2011). High phenotypic plasticity would allow *S. densiflora* to adjust important functional traits in response to variable environmental conditions, resulting in the ability to invade diverse habitats, a trait that has also been described for other invasive plants (e.g. Williams et al. 1995). Recent observations confirm that the invasive spread of *S. densiflora* in the Pacific Northwest region

of North America accelerated during the last two decades (e.g. Pickart 2001; Smith et al. 2001). These results are consistent with those recorded on the southwest Iberian Peninsula, where *S. densiflora* has invaded very different estuarine habitats (Nieva et al. 2001b), and a variety of phenotypes are recognized (Castillo et al. 2003; Nieva et al. 2005; Castillo et al. 2008).

In contrast to our results, Qing et al. (2011) reported differences in plant traits in a common garden experiment comparing native North American populations of *S. alterniflora* and invasive populations in China. This is perhaps due to genetic shifts that can play a vital role in the success of invasions. Our results

Fig. 5 Relationship between above-ground biomass (AGB) and leaf area index (LAI) and sediment gravel content, latitude and mean daily air temperature during last week before sampling for tussocks from five invasive populations of *Spartina*

densiflora along the Pacific Coast of North America. Populations: SF San Francisco Bay Estuary, HB Humboldt Bay Estuary, MR Mad River Estuary, GH Grays Harbor Estuary, VI Vancouver Island

point to a relatively low level of genetic variation for tussock architecture traits in invasive *S. densiflora* populations. This result is consistent with previous studies that recorded high genetic similarity between *S. densiflora* invasive populations (Ayres et al. 2008), which may be the result of genetic drift in genotypes introduced sequentially from one estuary to another. A genetic component influencing these traits due to local adaptation cannot be ruled out, however, since we found slight significant interpopulation differences in live and spiked shoot density after more than 2 year in a common environment. Furthermore, our common garden experiment may not necessarily have provided conditions for different genotypes to express distinct tussock-trait phenotypes (Thompson 1991).

In view of these results and those of companion studies (Castillo et al. 2014; Grewell et al. 2015), *S. densiflora* appears to be a halophyte with a high degree of phenotypic plasticity in tussock architecture and foliar traits that enables it to colonize a wide range of environmental variability in novel marsh habitats along the Pacific Coast of North America. Furthermore, our data support predictions (Bortolus 2006) that *S. densiflora* has the capacity to adjust and invade European salt marshes at higher latitudes than it currently occupies on the southwest of the Iberian Peninsula. *S. densiflora* appears to have the capacity to respond successfully to changes in the abiotic conditions of salt marshes driven by global climate change, such as increasing air temperature and estuarine salinity.

Fig. 6 Relationship between shoot height and sediment redox potential and mean daily global insolation for the sampling month, and between spiked shoot density and mean daily air temperature during last week before sampling for tussocks from

five invasive populations of *Spartina densiflora* along the Pacific Coast of North America. Populations: *SF* San Francisco Bay Estuary, *HB* Humboldt Bay Estuary, *MR* Mad River Estuary, *GH* Grays Harbor Estuary, *VI* Vancouver Island (Baynes Sound)

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